



Management and Conservation Article

Contrasting Activity Patterns of Sympatric and Allopatric Black and Grizzly Bears

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ABSTRACT The distribution of grizzly (*Ursus arctos*) and American black bears (*U. americanus*) overlaps in western North America. Few studies have detailed activity patterns where the species are sympatric and no studies contrasted patterns where populations are both sympatric and allopatric. We contrasted activity patterns for sympatric black and grizzly bears and for black bears allopatric to grizzly bears, how human influences altered patterns, and rates of grizzly–black bear predation. Activity patterns differed between black bear populations, with those sympatric to grizzly bears more day-active. Activity patterns of black bears allopatric with grizzly bears were similar to those of female grizzly bears; both were crepuscular and day-active. Male grizzly bears were crepuscular and night-active. Both species were more night-active and less day-active when ≤ 1 km from roads or developments. In our sympatric study area, 2 of 4 black bear mortalities were due to grizzly bear predation. Our results suggested patterns of activity that allowed for intra- and inter-species avoidance. National park management often results in convergence of locally high human densities in quality bear habitat. Our data provide additional understanding into how bears alter their activity patterns in response to other bears and humans and should help park managers minimize undesirable bear–human encounters when considering needs for temporal and spatial management of humans and human developments in bear habitats.

KEY WORDS activity budget, American black bear, brown bear, encounters, Global Positioning System (GPS), intra-guild predation, national park, *Ursus americanus*, *Ursus arctos*.

Historically, grizzly bears (*Ursus arctos*) were distributed throughout the Greater Yellowstone Ecosystem, but by the time the species was listed as threatened in 1975, they were restricted to an area within and adjacent to Yellowstone National Park, USA. During the 1980s and 1990s, grizzly bears expanded southward into Grand Teton National Park, Wyoming, USA (hereafter, Teton Park [Basile 1982; Blanchard et al. 1992; Schwartz et al. 2002, 2006]). Over the last decade, the northern half of Teton Park has been consistently occupied by grizzly bears, where they are now considered common (Pyare et al. 2004); as of 2006 grizzly bears had yet to recolonize the southern half of Teton Park. American black bears (*U. americanus*) historically and currently occur throughout the Greater Yellowstone Ecosystem. With the recolonization of grizzly bears into Teton Park, black bears are once again sympatric with grizzly bears in the north, but the 2 species remain allopatric in the south. This recolonization afforded us a rare opportunity to contrast patterns of activity between the 2 species and between black bear populations sympatric and allopatric to grizzlies.

Traditionally, community ecologists assumed that similar species must differ in some aspect of their traits or responses to the environment (i.e., their niches) to coexist in the same habitat (Chase 2005). Both grizzly bears and black bears are generalist omnivores with niche and diet overlap (Mattson et al. 2005). They evolved separately >3.5 million years ago,

but their ranges have only overlapped for about 13,000 years, potentially providing little time to coevolve mechanisms to reduce competition (Kruken and Anderson 1980, Leonard et al. 2000, Apps et al. 2006). Herrero (1978) suggested that aggression, large body size, and long claws for digging gave grizzly bears an advantage in open habitats, whereas smaller body size, recurved claws that allow tree climbing, and timid behavior of black bears were better adaptations to forested environments. Research suggests grizzly bears dominate at concentrated food sources (e.g., salmon [*Oncorhynchus* spp.] streams, carcasses, dumps), whereas black bears have an advantage when foods are small and dispersed (e.g., berries; Welch et al. 1997, Jacoby et al. 1999, Rode et al. 2001).

In addition to competing for shared resources, predators can influence activity patterns of prey. Intra-guild predation involves killing of species that use similar resources and are thus potential competitors (Polis et al. 1989). Intra-guild predation is important in applied ecological problems, such as conservation of mammalian carnivores (Polis and Holt 1992, Linnell and Strand 2000). Although black and grizzly bears are omnivorous, intra-guild predation of grizzly bears on black bears was documented (Palomares and Caro 1999, Gunther et al. 2002, Mattson et al. 2005).

There is a wealth of published literature detailing diel activity patterns of the 2 species, but most focuses on activity patterns for one species or the other and not both. Black bears are generally considered diurnal (Amstrup and Beecham 1976, Lindzey and Meslow 1977, Garshelis and Pelton 1980, Larivière et al. 1994, Holm et al. 1999),

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although they may become nocturnal in response to humans and food (Ayres et al. 1986, MacHutchon et al. 1998, Reimchen 1998). Grizzly bears are considered crepuscular or diurnal in North America (Stemlock and Dean 1986, Gunther 1990, McCann 1991, MacHutchon et al. 1998) and nocturnal in Europe (Roth and Huber 1986, Clevenger et al. 1990, Kaczensky et al. 2006, Moe et al. 2007), and they may alter these patterns in response to humans and food (Olson and Gilbert 1994, MacHutchon et al. 1998, Olson et al. 1998, Klinka and Reimchen 2002, Kaczensky et al. 2006).

Human developments (e.g., roads, campgrounds, lodges) impact both bear species. Spatial research addressing impacts where both species were studied concurrently suggests grizzly bears are more sensitive to human development than black bears and black bears may benefit spatially when humans encroach into high-quality grizzly habitat (Kasworm and Manley 1990, Apps et al. 2006). Similar research addressing temporal aspects of human development where the 2 species are sympatric is lacking.

As part of a comprehensive study investigating relationships among grizzly bears, black bears, and humans in Teton Park, we had the opportunity to study temporal activity patterns. In 2 study areas, one where black bears were sympatric and one where they were allopatric with grizzly bears, we examined 1) daily and seasonal activity patterns of both species, 2) how patterns differed among sexes, species, and study areas, 3) how human influences altered these patterns, and 4) the occurrence of bear–bear predation. Based on previous literature, we anticipated black bear and grizzly bear activity patterns would differ. We hypothesized that if different activity patterns between the 2 species evolved to reduce competition for shared resources, we would observe similar activity patterns between populations of black bears sympatric and allopatric with grizzly bears because black bears in our 2 study areas essentially constituted the same population, which was historically sympatric to grizzly bears. In contrast, different black bear activity patterns between areas would suggest a behavioral response to grizzly bears. If intra-guild predation influenced activity patterns, we hypothesized that black bears sympatric to grizzly bears would adjust activity patterns to avoid predation, whereas allopatric black bears would not; their patterns would be similar to grizzly bears. If cannibalism influenced activity, we hypothesized that smaller victims would adjust activity patterns to avoid larger potential killers. Thus, for both species, we expected activity patterns to differ between females and males.

Because humans are a dominant feature in Teton Park, we also investigated influences of open motorized roads and developments on temporal activity patterns. We hypothesized that both species would be less active near roads and developments when humans were present and that impacts of humans would be greater on grizzly bears (Apps et al. 2006). Finally, because grizzly bear predation on black bears has only been reported occasionally, we hypothesized grizzly bear predation would not be an important mortality factor for black bears in our sympatric study area.

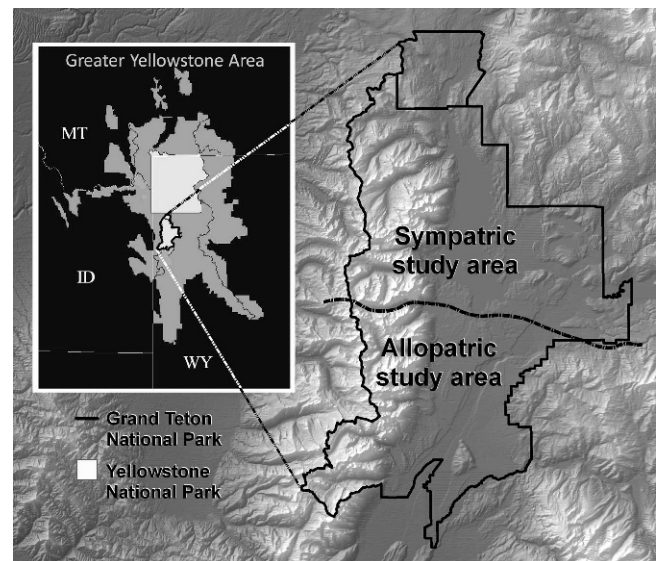


Figure 1. Grand Teton National Park, Wyoming, USA, showing study areas where black bears were sympatric and allopatric with grizzly bears, 2004–2006.

STUDY AREA

We conducted our study from April to November 2004–2006 within Teton Park where black bears were sympatric with and allopatric to grizzly bears. The study area included the upper Snake River drainage in a high-elevation valley, commonly called Jackson Hole, which was bounded by the Teton Range to the west, the Gros Ventre and Absaroka mountains to the east, the Yellowstone Plateau to the north, and the town of Jackson, Wyoming, to the south. Our sympatric study area included lands north of Leigh Canyon in the Teton Range and Spread Creek in the valley floor (Fig. 1). Our allopatric study area encompassed the southern part of Teton Park roughly south of Leigh Canyon to the Park's southern border.

In both study areas, elevation ranged from 1,890 m in the valley floor to 4,197 m atop surrounding peaks. Climate was characterized by long, cold, snowy winters and short, cool summers. The 30-year (1971–2000) mean high and low temperatures were -3.1°C and -18.6°C , respectively, in January and 24.7°C and 2.6°C , respectively, in July at Jackson Lake Dam near the center of Teton Park (Western Regional Climate Center 2010). Approximately 70% of precipitation typically fell as snow.

Patterns of precipitation and temperature produced predictable vegetation patterns (Marston and Anderson 1991). Low elevations ($<1,900\text{ m}$) supported foothill grasslands or shrub-steppe communities. With increasing moisture, open stands of Douglas-fir (*Pseudotsuga menziesii*) were common. Lodgepole pine (*Pinus contorta*) formed the lowest elevation forest community at around 1,900–2,200 m and dominated the extensive Yellowstone Plateau at mid-elevations (2,400 m), where poor rhyolite-based soils were prevalent (Patten 1963, Waddington and Wright 1974, Despain 1990, Romme and Turner 1991). With increasing elevation, spruce–fir or subalpine forests dominated. White-

bark pine (*Pinus albicaulis*) characterized the upper tree line around 2,900 m (Patten 1963, Waddington and Wright 1974, Despain 1990). Alpine tundra occurred at the highest reaches of all major mountain ranges.

METHODS

Trapping and Collaring

We used culvert traps to capture black and grizzly bears (Blanchard 1985). Trapping occurred within Teton Park, mainly on service roads closed to public access, and adjacent to the west shoreline of Jackson Lake, which was accessible by boat. Trap sites were remote enough to effectively eliminate direct human disturbance. The spatial extent of our telemetry locations suggested we had a reasonable distribution of individuals throughout the park. Our animal handling procedures were approved by the Animal Care and Use Committee of the United States Geological Survey, Biological Resources Division, and conformed to the Animal Welfare Act and United States Government principles for the utilization and care of vertebrate animals used in testing, research, and training. All field work was under permits issued by the United States Fish and Wildlife Service and the National Park Service.

We fitted all captured bears, except dependent offspring or very small subadult black bears, with Telonics Spread Spectrum (SS) Global Positioning System (GPS) collars (Telonics, Inc., Mesa, AZ), a programmable breakaway collar release (Telonics, Inc.), a biodegradable canvas spacer, and a motion sensor that reduced transmitter pulse rate if stationary for 4–5 hours. Each transmitter also contained a -15° head to tail activity switch (e.g., see below) that tallied seconds of switch closure accumulated during a 15-minute interval just prior to the GPS fix attempt. The number returned was a percentage of total seconds of switch closure during the collection interval at 0.5% resolution. These activity counts were reflective of the bear's head-up head-down movement just prior to each GPS fix or attempted fix and have been shown to be useful in discriminating between active and resting bears based upon activity count (Schwartz et al. 2009).

We set collars to maximize the number of fixes over the duration of deployment. The manufacturer recommended a longer fix interval each year of our study. As a consequence, our fix intervals varied from 35 minutes to 190 minutes (for details see Schwartz et al. 2009). We programmed GPS units to search for available satellites for up to 180 seconds. If a successful fix was not obtained, units turned off until the next scheduled fix attempt. Units were off during the anticipated denning season (15 Nov–14 Apr or 31 Oct–14 Apr for grizzly and black bears, respectively). An integrated very high frequency (VHF) transmitter functioned daily and independently of the SS GPS unit. We flew telemetry flights weekly from late April through early November to retrieve data. During each telemetry flight, the previous week's GPS data were retrieved and stored on a laptop computer in the aircraft.

Activity Patterns

We chose bear-year (one bear's data for one active season) as our sample unit. We plotted mean activity for each bear-year

by hour each month against the grand mean to determine if repeated measures from the same bear over multiple years tended to cluster (suggesting a lack of independence) or were dispersed among bears. We also contrasted standard deviations of hourly activity calculated with bear-year and bear (over all yr sampled) as the sample unit. We concluded that using bear-year as our sample unit was not likely to bias either our mean activity estimates or estimates of uncertainty associated with them (see Results).

We used activity counts recorded in collars to contrast daily activity patterns between species, sexes, and study areas. Because collars recorded activity counts regardless of fix success, we included all fix attempts, thereby allowing for a continuous sample (determined by fix interval) of activity for each bear. We used the regression approach of Murtaugh (2007) and fit no-intercept models to activity count. Resulting coefficient estimates were sample mean counts and standard errors for each bear-year for each hour. We summarized results for each species, sex, and study area category using the weighted average of the bear-year-specific regression coefficients, with weights proportional to reciprocals of squared standard errors for individual fits (Murtaugh 2007).

We defined crepuscular as the period of morning twilight to sunrise and sunset to evening twilight. We partitioned twilight into 3 categories. Civil twilight began in the morning when the geometric center of the sun was 6° below the horizon and ended at sunrise and again in the evening at sunset and ending when the sun was 6° below the horizon. During civil twilight, humans could easily distinguish objects and carry out activities without artificial light. Brightest stars and planets appear during civil twilight. Nautical twilight was when the geometric center of the sun was 12° to 6° below the horizon, during which the horizon appeared indistinct and terrestrial objects could be made out, but artificial light was required to carry on activities. Astronomical twilight was when the sun was 18° to 12° below the horizon and sky illumination was unnoticeable. We defined diurnal as the time between sunrise and sunset and nocturnal between evening twilight and morning twilight. We used sunrise, sunset, and twilight tables for Old Faithful Lodge, Wyoming (Naval Oceanographic Portal 2010). We obtained measured air temperature hourly from a fixed station roughly centered in the southern, allopatric study area (Meso West 2009; Fig. 1); temperature patterns were reflective of areas our marked bears used.

To test for differences between sex, species, and study areas, we contrasted 8 group pairings: 1) male versus female grizzly bears, 2) male grizzly bears versus sympatric black bears [both sexes], 3) male grizzly bears versus allopatric black bears [both sexes], 4) female grizzly bears versus sympatric black bears [both sexes], 5) female grizzly bears versus allopatric black bears [both sexes], 6) sympatric versus allopatric black bears [both sexes], 7) male versus female sympatric black bears, and 8) male versus female allopatric black bears. We fit 4 regression models for each comparison. The response variable in each case was the difference in

Table 1. Model comparison and AIC_c (Akaike's Information Criterion adjusted for small sample size) results contrasting differences in activity patterns between sympatric and allopatric black and grizzly bears in Grand Teton National Park, Wyoming, USA, 2004–2006.

Comparison no. and group	AIC _c score ^a			
	Model 1	Model 2	Model 3	Model 4
1. Grizzly bear M vs. grizzly bear F	191.65	142.41	119.67	118.66
2. Grizzly bear M vs. sympatric black bear (both sexes)	205.43	157.50	148.53	136.54
3. Grizzly bear M vs. allopatric black bear (both sexes)	197.38	148.07	137.01	125.99
4. Grizzly bear F vs. sympatric black bear (both sexes)	151.84	123.69	132.20	117.40
5. Grizzly bear F vs. allopatric black bear (both sexes)	123.97	110.77	119.63	108.64
6. Black bear sympatric vs. black bear allopatric (both sexes)	128.08	105.13	105.78	100.11
7. Black bear M vs. black bear F (sympatric area)	97.45	91.76	97.91	93.05
8. Black bear M vs. black bear F (allopatric area)	145.85	138.77	143.20	136.00

^a Regression models (see Methods) included fitting means with uncorrelated (1) and correlated errors (2), and using radian-transformed hours with uncorrelated (3) and correlated (4) errors. The lowest AIC_c score for model 1 or 2 should be interpreted as no difference in temporal activity patterns, whereas a low score for models 3 or 4 indicates a temporal difference between groups.

mean activity count between the 2 groups. The first model fit the mean with uncorrelated errors. The model was

$$y_t = \beta_0 + \varepsilon_t$$

where y_t was the difference in mean activity count at time t , $t = 0, \dots, 23$, β_0 was the overall true mean difference, and ε_t were independent and identically normally distributed with mean = 0 and variance = σ^2 .

The second model was the same as model 1, but accounted for correlated errors using the following formula:

$$\varepsilon_t = \rho\varepsilon_{t-1} + \mu_t$$

where $|\rho| < 1$ and μ_t were independent and identically normally distributed with mean = 0 and variance = σ^2 . This model followed a first-order autoregressive AR(1) process.

In the third and fourth models, we treated hour as a circular variable by transforming to radians (each hr corresponded to 15°) and taking the sine and cosine as suggested by Fisher (1993):

$$y_t = \beta_0 + \beta_1 \sin(\text{hour}) + \beta_2 \cos(\text{hour}) + \varepsilon_t$$

We treated errors as uncorrelated in model 3 and accounted for correlated errors in model 4 as above.

Because of sample size limitations, we chose to fit these 4 simple models and avoid issues of sample size:parameter estimation ratios. For example, the fourth model had 5 parameters, with a sample size:parameter ratio of about 5. We estimated all parameters using maximum likelihood methods. We compared the 4 models using Akaike's Information Criterion (AIC) adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We concluded there were no differences in temporal (24-hr) activity patterns (e.g., shape of the 2 curves was the same) for group comparisons if AIC_c scores were lowest for models 1 or 2. We concluded overall activity levels differed (e.g., one group was more active, but 24-hr patterns were similar) if the 95% confidence interval for the mean difference did not overlap zero. We interpreted low AIC_c scores for models 3 or 4 as evidence of different temporal patterns (e.g., shape of the 24-hr activity curves differed). We used normalized residuals for diagnostics, which should be independent and

identically distributed as standard normal random variables (Pinheiro and Bates 2000). We fit models using the *gls* function available in the *nlme* package in the R statistical programming language (R Development Core Team 2010).

To summarize monthly activity patterns, we aggregated activity counts for each bear-year each month and hour. We summarized activity patterns ($\bar{x} \pm \text{SE}$) by species, sex, and study area.

We measured distance from each successful telemetry location to the nearest road or developed site. Our road coverage included paved and gravel roads open to vehicle travel. Developed sites included campgrounds, lodges, restaurants, stores, visitor centers, ranger stations, park housing, and other facilities regularly used by park visitors and staff. We categorized distance measures into 6 ordinal bins of 1-km width (0–1 km, 1–2 km, ..., 4–5 km, and >5 km). We used data for June–August because we collared most bears during this period, activity patterns were similar among these months, and this was the period of peak human summer visitation.

RESULTS

In our sympatric study area, from 2004 to 2006, we deployed SS collars on 29 individuals (10 grizzly [6 M, 4 F] and 19 black bears [11 M, 8 F]). Median (range) age of grizzly and black bears when first captured was 9 (3–17) years and 7 (3–25) years, respectively. We collected 16 grizzly and 25 black bear-years of data over 6,669 days. Collars attempted to collect 92,438 fixes, with 76,796 (83.1%) successful GPS locations recorded. In our allopatric study area from 2005 to 2006, we deployed SS collars on 5 male and 5 female black bears. Median age (range) of these bears when first captured was 6 (3–13) years. We collected 20 black bear-years of data over 1,880 days. Collars attempted 14,477 fixes, with 10,008 (69.1%) successful.

For group comparisons, our models that accounted for correlated errors returned lower AIC_c scores than those not considering them (Table 1); our diagnostic plots revealed our data met assumptions (except where noted). We found strong evidence that temporal activity patterns differed between male and female grizzly bears; males were more night-active and females more day-active (Table 1;

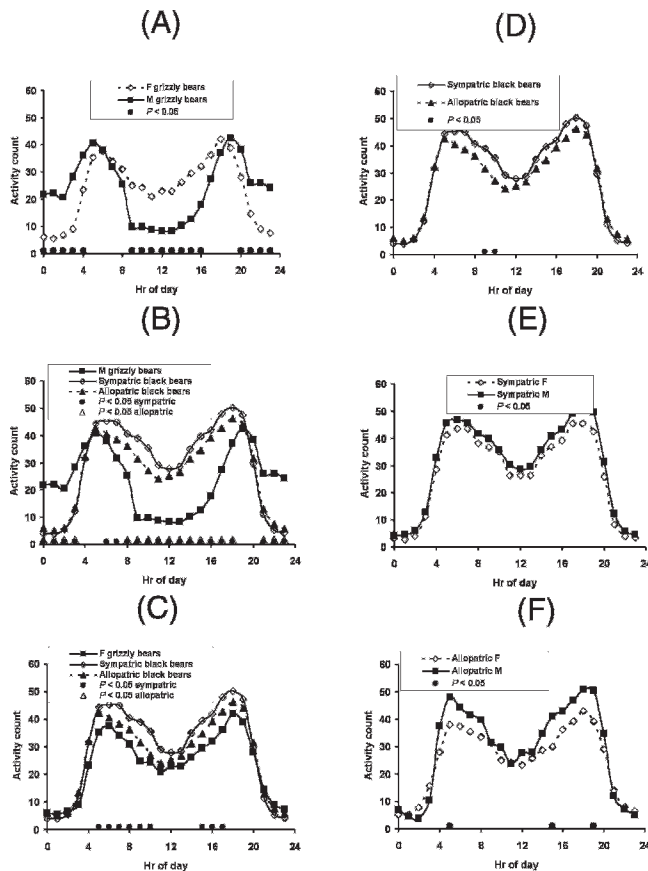


Figure 2. Mean activity counts by hour of day (Mountain Standard Time) obtained from Global Positioning System collars deployed on bears in Grand Teton National Park, Wyoming, USA, 2004–2006, contrasting activity of (A) male and female grizzly bears, (B) male grizzly bears and sympatric and allopatric black bears [both sexes], (C) female grizzly bears and sympatric and allopatric black bears [both sexes], (D) sympatric and allopatric black bears [both sexes], (E) sympatric male and female black bears, and (F) allopatric male and female black bears. Solid dots and opened triangles at bottom show paired hourly mean differences at $P = 0.95$. We summarized data with bear-year as the sample ($n = 16$ and 25 for sympatric grizzly and black bears, respectively, and $n = 10$ for allopatric black bears).

Fig. 2A). Male grizzly bears were also more night-active when compared to both sympatric and allopatric black bears, which were more day-active (Table 1; Fig. 2B).

We also concluded that sympatric black bears were more day-active than female grizzly bears because model 4 had the lowest AIC_c score and the ΔAIC_c for the next closest model was 6.29 (Table 1; Fig. 2C). We found weak evidence that allopatric black bears were more day-active than female grizzly bears. Model 4 had the lowest AIC_c score, but model 2 was also a plausible candidate ($\Delta AIC_c = 2.1$ [Table 1; Fig. 2C]). Sympatric black bears were also more day-active than allopatric black bears (Table 1; Fig. 2D).

Our results suggested that temporal activity patterns did not differ between male and female black bears in the sympatric study area (Table 1), but overall level of activity was higher for males (mean difference $[F - M] = -2.95$, 95% CI = -4.43 to -1.46). Temporal activity patterns differed between male and female black bears in the allopatric study area (Table 1). Model 4 had the lowest AIC_c score, although model 2 was similar ($\Delta AIC_c = 2.77$).

Diagnostics for model 4 revealed that one observation had a large standardized residual of around -3 ; the residual plot for model 2 suggested a better fit. Thus, we concluded that temporal patterns between sexes in our allopatric study area may have been different, but evidence was weak.

Monthly activity patterns for both species were similar. Just after den emergence in spring (Apr) and just prior to den entrance in autumn, both species were inactive most of the day, with peak activity in late afternoon (Fig. 3). In May, activity increased in afternoon and to a lesser extent in morning. From June through September (Oct for grizzly bears), a definite bimodal pattern was evident, with activity peaks near sunrise and just prior to sunset. Grizzly bears showed high levels of activity from June through September, which declined in October and November (Fig. 3). Black bears displayed a similar pattern, with high levels of activity from June through August, which declined from September through October (Fig. 3).

Both species exhibited major shifts in activity patterns during crepuscular periods. For example, in July morning activity typically began when it was still dark (prior to astronomical twilight), reaching peak activity during civil twilight (very near sunrise), then declining to midday (Fig. 4). Activity increased shortly after noon, typically peaking in evening prior to sunset (Fig. 4); activity declined rapidly during the evening crepuscular period, reaching its lowest values after astronomical twilight when it was dark. However, male grizzly bears were more active at night than midday. Female grizzly bears and black bears were more active midday and less active at night.

Grizzly bears were more night-active (2100–0200 hr) and less day-active (0500–1700 hr) when they were <1 km from a development (Fig. 5A). Peak activity shifted 1 hour earlier in the morning and 1 hour later in the evening near human developments. Activity counts suggested grizzly bears were, on average, inactive (resting) for about 8 hours during the day (0900–1600 hr) when <1 km from a developed site but were, on average, active (foraging or traveling) during this same time when >5 km from a developed site. Black bears appeared less affected by developments, becoming active 1 hour earlier in morning, but not shifting activity after sunset. Black bears were also slightly less active midday when near developed sites, but only 1 hour (1100 hr) was statistically lower (Fig. 5B). We detected similar but reduced impacts as bears were >1 – 2 km from developments. The influence of roads on activity patterns was similar to that for distance to developments for both species (Fig. 6A, B).

DISCUSSION

Our results demonstrated that bears alter activity patterns in response to other bears and humans. Based on these findings, we rejected our first hypothesis and concluded that black bears alter activity patterns where they are sympatric with grizzly bears. Sympatric black bears were more day-active than either male or female grizzly bears. Sympatric black bears were also more day-active than allopatric black bears. If differences in activity patterns

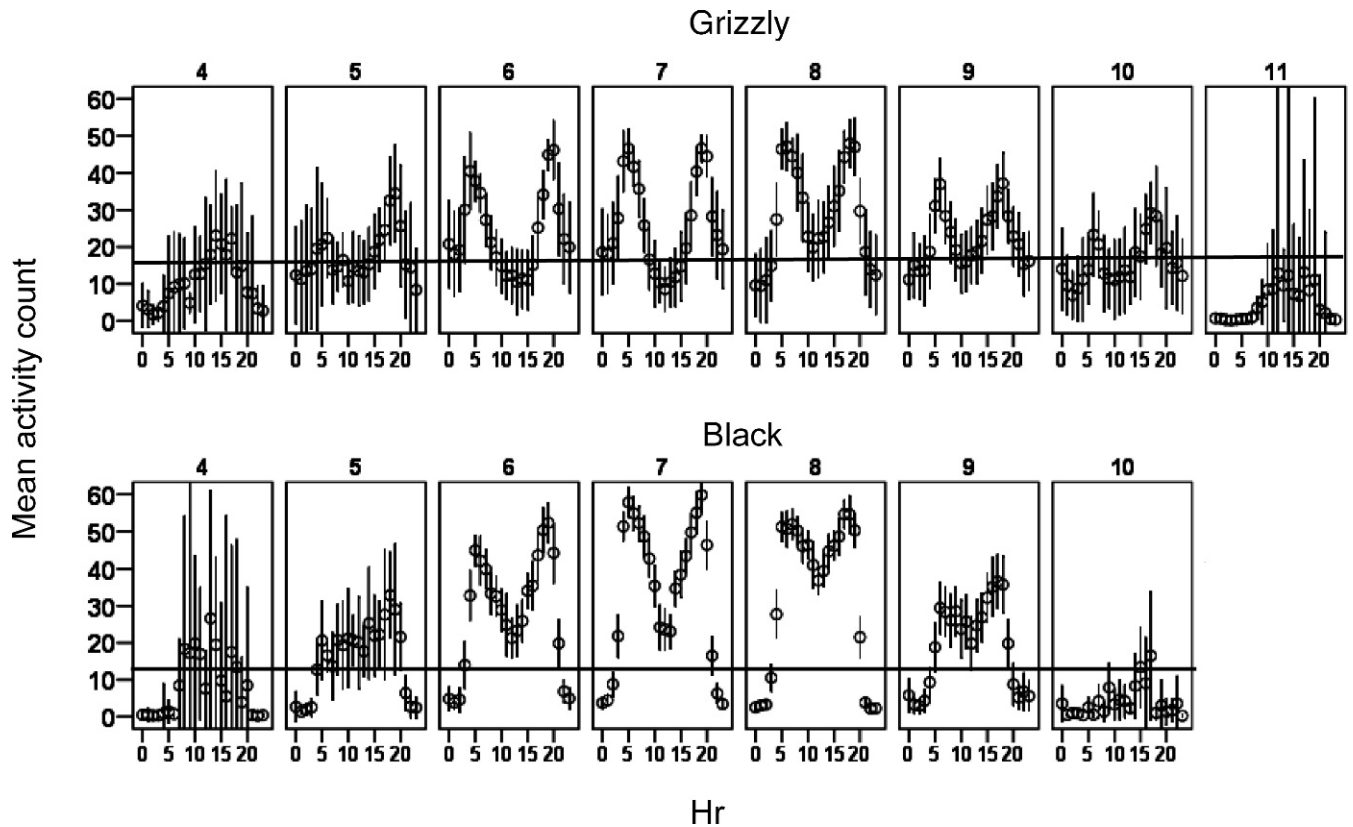


Figure 3. Mean hourly activity count (95% CI) from Global Positioning System collars deployed on sympatric grizzly (months Apr–Nov, e.g., 4–11) and black (months Apr–Oct, e.g., 4–10) bears in Grand Teton National Park, Wyoming, USA, 2004–2006. We summarized data with bear-year as the sample ($n = 16$ grizzly and 25 black bears). The black horizontal line represents the predicted breakpoint (Schwartz et al. 2009) between resting (below the line) and active (above line) bears.

between black and grizzly bears were a product of evolutionary pressures to reduce competition, we hypothesized that sympatric and allopatric black bear populations would behave similarly. Historically, black bears were

sympatric with grizzly bears throughout the Greater Yellowstone Ecosystem, and it was not until the 1940s that grizzly bears were extirpated from Teton Park (Pyare et al. 2004). According to reported sightings, grizzly bears began

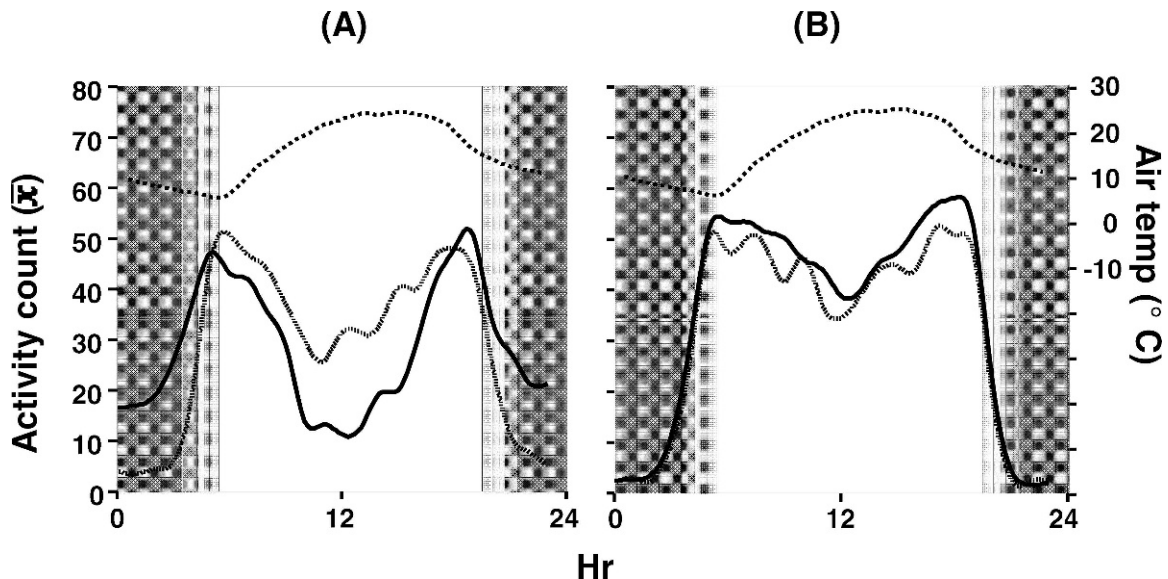


Figure 4. Mean hourly activity count during July for (A) male (solid black line) and female (gray hashed line) grizzly bears, and (B) sympatric black bears in Grand Teton National Park, Wyoming, USA, 2004–2006. Gray shaded areas represent the time after sunset but before sunrise. Night time is represented by the darkest gray color, with progressively lighter shades of gray representing astronomical, nautical, and civil twilight. Temperature values (dashed line) are mean hourly temperatures during July for the 3-year period. We summarized data by bear-year ($n = 7$ M and 9 F grizzly bears, and $n = 12$ M and 13 F black bears).

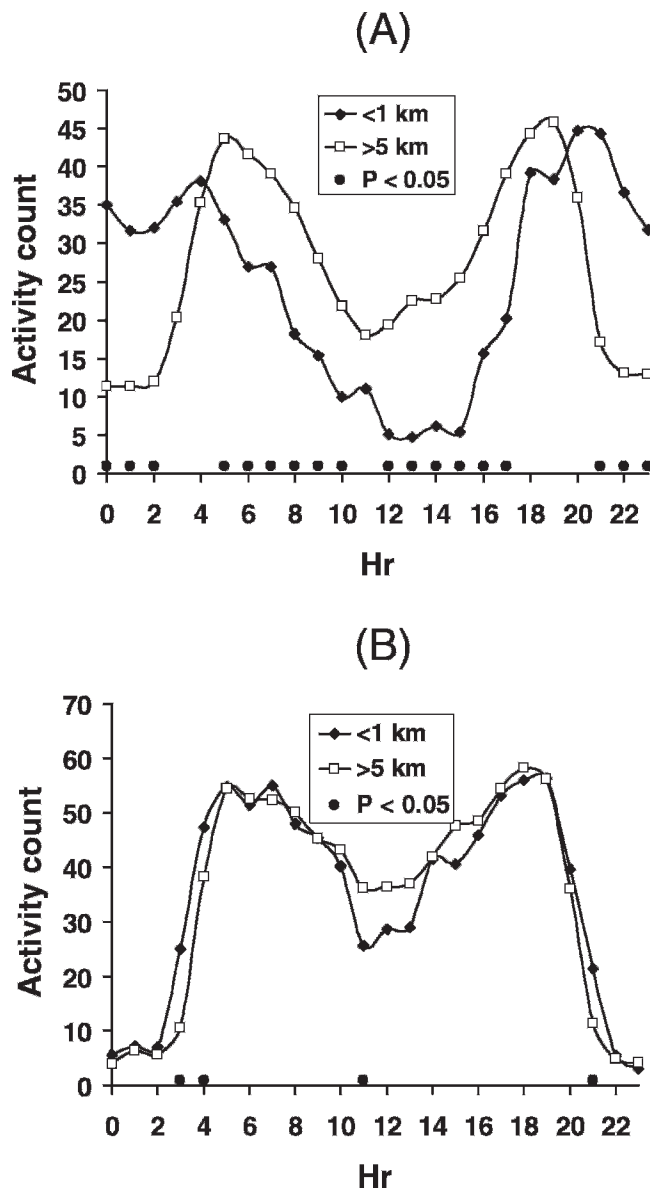


Figure 5. Mean activity counts by hour during June–August for (A) grizzly, and (B) sympatric black bears in Grand Teton National Park, Wyoming, USA, 2004–2006, when near and far from developed sites. Solid dots at bottom show paired hourly means where the 95% confidence interval did not overlap. We divided distance counts into 6 bins of equal widths of 1 km (e.g., 0–1 km, 1–2 km, ..., 4–5 km, and >5 km). We summarized data by bear-year ($n = 16$ and $n = 25$ grizzly and black bears, respectively).

to recolonize Teton Park in the 1970s, but rapid expansion did not occur until the late 1980s through the 1990s (Pyare et al. 2004). Hence, our sympatric black bear population coexisted with grizzly bears for only about 20 years. We concluded that the presence of grizzly bears elicited a behavioral response by black bears. The fact that sympatric black bears were more day-active than allopatric black bears further supported this conclusion. Our conclusions are also supported by earlier studies that speculated on the diurnal nature of black bears as a mechanism for avoiding conflicts with grizzly bears (Craighead and Craighead 1972, Schleyer 1983).

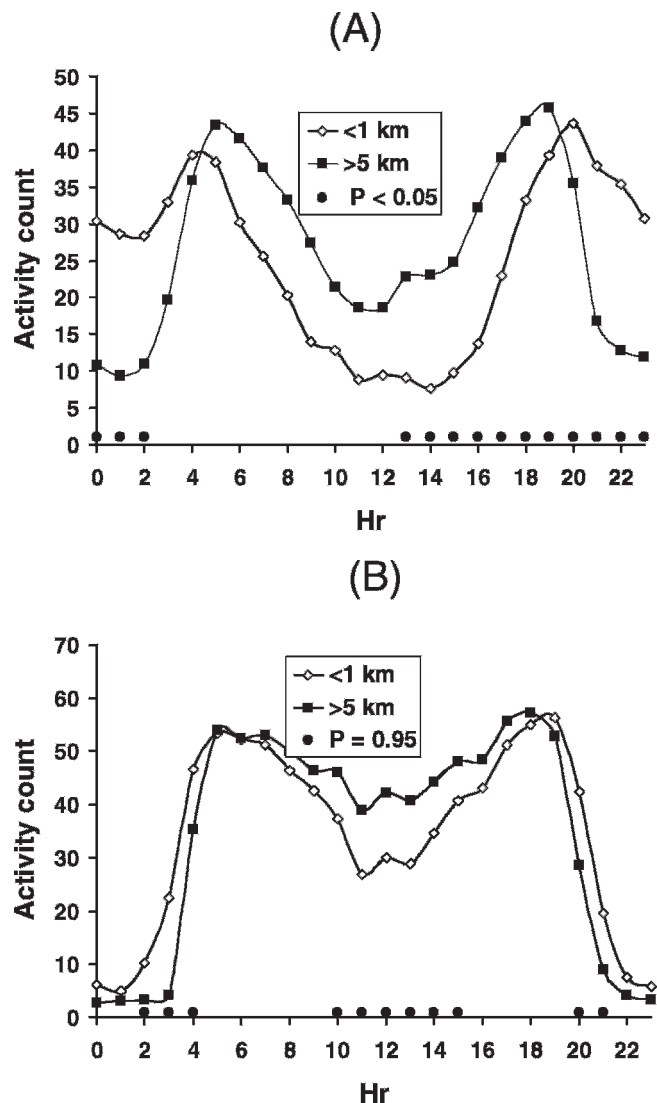


Figure 6. Mean activity counts by hour during June–August for (A) grizzly, and (B) sympatric black bears in Grand Teton National Park, Wyoming, USA, 2004–2006, when near and far from roads. Solid dots at bottom show paired hourly means where the 95% confidence interval did not overlap. We divided distance counts into 6 bins of equal widths of 1 km (e.g., 0–1 km, 1–2 km, ..., 4–5 km, and >5 km). We summarized data by bear-year ($n = 16$ and $n = 25$ grizzly and black bears, respectively).

We documented 2 cases of marked black bears being killed by grizzly bears. Although we lack estimates of density for the 2 bear species, trapping records from the Interagency Grizzly Bear Study Team in the Greater Yellowstone Ecosystem (C. Dickinson, United States Geological Survey, personal communication) suggest that in areas where grizzly bear catch rates are high, black bear catch rates are very low. The reverse appears to be the case on the edge of occupied grizzly bear habitat, where trapping grizzly bears is very difficult but nontarget black bears are commonly caught. We thus hypothesized that intra-guild predation by grizzly bears may limit black bear density and that black bear numbers may decline in Teton Park as grizzly bears continue expanding south and eventually recolonize the southern part of the Park.

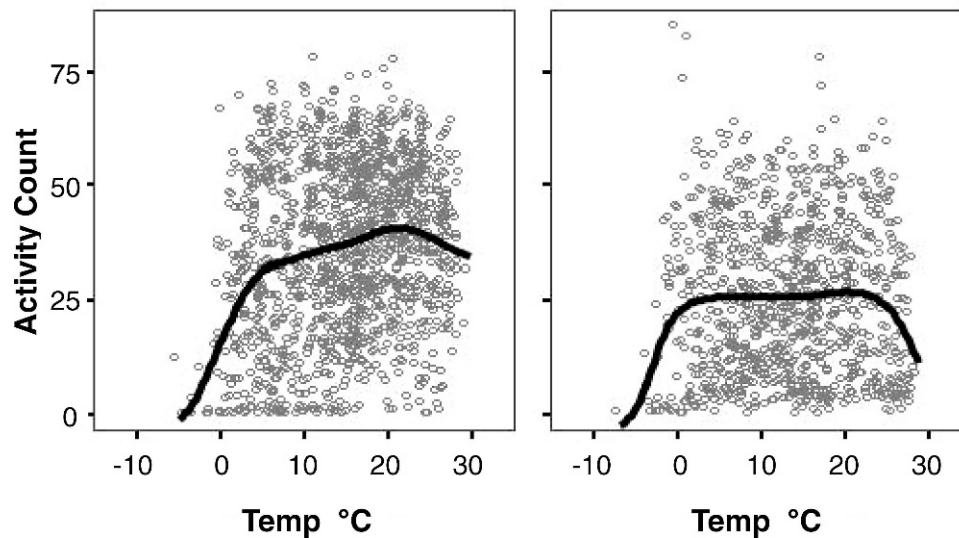


Figure 7. Scatter plot of daytime (sunrise to sunset) activity counts and air temperatures for black (left) and grizzly (right) bears in Grand Teton National Park, Wyoming, USA, 2004–2006. The solid line (local linear regression with a band width of 1.0; SPSS 15.0) illustrates the general trend within the data, which we summarized with bear-year as the sample ($n = 16$ and $n = 25$ grizzly and black bears, respectively).

Although it is difficult to demonstrate cause–effect relationships with observational studies, we speculate female grizzly bears may be more active than males during the day to reduce the risk of conflict with males. On occasion, grizzly bears kill one another. In a review of the literature McLellan (1994) documented that adult males were implicated as killers in nearly 78% of the 27 cases where age and sex of the killer was known. Of 57 cases of intra-specific killing, cubs of the year were the most frequent victims (44%, $n = 25$), but adult females were also killed (18%, $n = 10$). Adult females also have been observed killing cubs (Hessing and Aumiller 1994). McLellan and Shackleton (1988) showed that yearlings and female grizzly bears with cubs use habitats near roads more than do other bears, possibly to avoid male bears. Female grizzly bears with dependent young also fish at salmon spawning streams at different times than males, suggesting temporal avoidance of males (Olson 1993). Female black bears were similarly more day-active than males in our allopatric study area but not in the sympatric study area. We therefore can neither accept nor reject our hypothesis regarding cannibalism (e.g., smaller victims adjust activity to avoid larger killers).

Male grizzly bears in our study area were primarily nocturnal. Aside from humans, adult male grizzly bears have no predators. Grizzly bears in the western United States were severely persecuted by European settlers and were exterminated from >98% of their historic range (Servheen 1999, Schwartz et al. 2003), so being night-active could reduce vulnerability to humans. European brown bears are night-active, and it has been speculated that this behavior is a direct result of centuries of human persecution (Swenson 1999).

If, on the other hand, male grizzly bears are night-active to maximize energy intake, then there should be an advantage to being nocturnal. Male Yellowstone grizzly bears are mostly carnivorous, with about 79% of their diet composed

of meat consumed as ungulate carrion, neonatal ungulates, usurped or scavenged ungulate kills of gray wolves (*Canis lupus*) and human hunters, and adult ungulates as prey (Schleyer 1983, Gunther and Renkin 1990, Mattson et al. 1991, Jacoby et al. 1999). Yellowstone grizzly bears have been observed diurnally obtaining meat through each of these methods, but relative rates or efficiencies of securing meat during day versus night are unknown. African lions (*Panthera leo*; Schaller 1972) and spotted hyenas (*Crocuta crocuta*; Kruuk 1972) mainly hunt at night because of superior night vision and reduced heat stress. We are unaware of studies that detail night vision in grizzly bears, but our results suggested reduced midday activity in both bear species when ambient temperatures exceeded 20° C (Fig. 7). However, we do not think male grizzly bear were night-active to avoid heat stress because they were also night-active during spring and autumn when daytime temperatures were cool (Fig. 3).

Both bear species became active earlier in the morning and were less active during midday near roads or developments. Grizzly bears also were more night-active when close to roads and developments. These results add to the understanding of effects of roads and developments on bears. Earlier research addressed the spatial impact of roads on bears (Mattson et al. 1987, McLellan and Shackleton 1988, Mace et al. 1996). Furthermore, because previous studies sampled mostly using VHF telemetry, data were temporally biased by patterns of favorable weather for flying light aircraft (e.g., mornings with good visibility). Because we used GPS collar data generated continually we found that bears did not entirely avoid areas near roads; rather, bears adjusted their active periods when near roads and developments to times when humans in these areas were less active. Other studies have similarly shown that both bear species are more nocturnal in areas where human activity is high (Ayres et al. 1986, Gibeau et al. 2002, Beckman and Berger

2003, Kaczensky et al. 2006). Our results, coupled with work of others, strongly suggested bears adjust temporal patterns of activity in response to humans. This shift suggests that bears perceive humans as a threat or nuisance and, thus, bears adjust their activity similarly to how they appear to adjust activity in response to larger, potentially predatory bears.

In national parks, where bear densities are often high, management emphasis is placed on both wildlife conservation and providing human recreation (e.g., U.S. National Park Service 1916), often resulting in elevated levels of human development in quality wildlife habitats. Two effects of this convergence are evident: 1) species sensitive to human disturbance can be displaced from preferred habitats, and 2) in certain areas the probability for undesirable interactions between humans and dangerous animals increases. Indeed, attacks by bears on humans in North America are disproportionately more frequent in national parks, most being the result of sudden encounters between hikers and grizzly bears that react defensively to protect young or a food source (Herrero 2002). In our study area, 5 individuals received serious injuries during grizzly bear attacks from 1994 to 2007. Each attack occurred during a period of high bear activity we identified, and all but one attack was the result of a defensive reaction by the bear. The exception was a lone cross-country skier who was attacked at night in an apparent investigative or predatory situation in which the bear departed after inflicting a few deep bites.

In Teton Park, human trail use is reflective of daily recreation patterns during summer and is generally described by a symmetrical bell-shaped curve with the lower bound at sunrise, the upper bound at sunset, and the peak equidistant between these (S. Cain, National Park Service, unpublished data). The peak in human use coincides with the midday nadir in bear activity we observed, but tails overlap periods of high bear activity, suggesting that early and late recreationists are at higher risk of bear encounters. This information could be used to regulate certain high-risk human activities in areas of high bear density. For example, reports of grizzly bear attacks on cyclists have recently escalated (e.g., Herrero and Herrero 2000). It has been suggested that, owing to a focus on traveling at inherently higher speeds, cyclists have an increased risk of sudden encounters with bears, particularly when conditions allow quiet travel (Herrero and Herrero 2000, Herrero 2002). In our study area, where bike paths through grizzly bear habitat have been proposed, restricting bicycle use to periods when bears are less active could have tangible benefits.

MANAGEMENT IMPLICATIONS

Our observations of grizzly and black bear activity patterns provide a baseline for contrasting activity patterns among sympatric and allopatric black and grizzly bears elsewhere, reveal potential changes in black bear behavior when sympatric with grizzly bears, and provide important insights into how bears negotiate human developments during their daily activities. In highly managed areas with both intense bear and human use (e.g., salmon fishing areas, national

parks), it may be practical to temporally separate humans and bears by allowing human access when bears are less active (during the day), while reserving crepuscular and night periods for bears. On the other hand, in areas where bear density is high, spatially separating human activities and developments that tend to have high levels of human activity both day and night must be considered to afford bears necessary foraging opportunities. We recommend other researchers incorporate activity counters into their telemetry systems to further refine our understanding of the influences of humans on bear activity patterns.

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